

Research Article

A laboratory study of potential effects of the invasive round goby on nearshore fauna of the Baltic Sea

Meagan N. Schrandt^{1,2,*}, Laura C. Stone^{1,2}, Brian Klimek^{1,2}, Saara Mäkelin³, Kenneth L. Heck Jr.^{1,2}, Johanna Mattila^{4,5} and Heidi Herlevi⁴

¹Department of Marine Sciences, University of South Alabama, Mobile, Alabama 36608, USA

²Dauphin Island Sea Lab, 101 Bienville Blvd., Dauphin Island, Alabama 36528, USA

³Department of Environmental Sciences, University of Helsinki, FI-00014, Helsinki, Finland

⁴Department of Biosciences, Environmental and Marine Biology, Åbo Akademi University, Tykistökatu 6, FI-20520 Turku, Finland

⁵Department of Aquatic Resources, Swedish University of Agricultural Sciences, Kustlaboratoriet, Skolgatan 6, SE-742 42 Öregrund, Sweden

*Corresponding author

E-mail: mschrandt@disl.org

Received: 28 March 2015 / Accepted: 2 February 2016 / Published online: 30 March 2016

Handling editor: Henn Ojaveer

Abstract

In the Baltic Sea, species diversity is relatively low and the introduction of new predator species can have large direct and indirect impacts on native species – both prey and potential competitors. The alien round goby *Neogobius melanostomus* Pallas, 1811 was introduced to the Baltic Sea in the early 1990s and is now well-established. We examined the feeding habits of male round gobies from the Åland Islands, Finland, where round gobies were first recorded in 2011. Specifically, we tested whether small round gobies (≤ 165 mm TL) showed size and/or species preferences (using Manly's selectivity index) for two abundant bivalve prey items, the blue mussel *Mytilus trossulus* Gould, 1850 and the Baltic clam *Macoma balthica* Linnaeus, 1758. When offered two sizes of clams, small round gobies did not show a prey preference. When offered two sizes of mussels, round gobies selected for small mussels (6 – 9 mm) and against large (10 – 13 mm) mussels. When offered both bivalve species and sizes simultaneously (four prey options), round gobies selected for small blue mussels and against large clams. Combined, these results suggest that small round gobies will selectively feed on the preferred prey if available and if not, their feeding will reflect the availability of various prey items in the environment. In addition, round gobies consumed small (≤ 38 mm TL) individuals of the native flounder *Platichthys flesus* Linnaeus, 1758. Round goby and flounder have the potential to overlap in habitat use and previous literature has suggested a diet overlap between the two; however, this is the first evidence of direct predation on flounder by round gobies.

Key words: *Neogobius melanostomus*, Baltic clam, blue mussel, European flounder, invasive fish, predator-prey interaction, prey preference, size selectivity

Introduction

The Baltic is a semi-enclosed shallow sea characterized by physical, chemical and biological gradients. Salinity stress and physical disturbance lead to reduced species diversity in the Baltic (Kautsky and Svensson 2003), but there is a mixture of marine and freshwater species as well as relicts from glacial periods (Voipio 1981). Because the Baltic Sea has relatively low diversity, and therefore low redundancy within its food web, understanding top down effects is important for taking actions to promote the system's ecological health. Predator-

prey relationships can play a major role in structuring aquatic food webs and ecosystems. Areas of the Baltic that have lost major herbivores or predators, whether naturally or human-induced, have undergone substantial changes and exhibit altered functionality (e.g. Eriksson et al. 2009; Casini 2013). But not only the loss of species can induce major changes in an ecosystem; the addition of novel species can also have a profound effect.

Invasive species can alter food webs, ecosystems, and economies. Typically, invasive species thrive because the new system lacks natural predators to control their populations and they can initially wreak

havoc on the balance of the system by consuming native species; competing with them for food, space, or other resources; and introducing diseases. In the marine realm, a global increase in marine traffic during the last century has increased species introductions to coastal areas (Carlton 1996; Ruiz et al. 1997). In the Baltic Sea alone, invasion rates have increased since the 1950s and, as of 2010, at least 119 alien species were recorded (Zaiko et al. 2011).

The round goby *Neogobius melanostomus* Pallas, 1811 is an invasive, predatory fish species, and its invasive characteristics have been well-studied (see review by Kornis et al. 2012). The round goby is native to the Ponto-Caspian region and has since spread to the Great Lakes in North America and throughout Europe, likely as a consequence of shipping. This bottom-dwelling fish was first reported in the Baltic Sea in the Gulf of Gdansk in 1990 and first discovered in the Gulf of Finland (east of Åland Islands, Finland) in 2005 (Ojaveer 2006). The round goby has formed a self-reproducing population in the Gulf of Finland (Järv et al. 2011) and is typically most abundant in rocky habitats (Kornis et al. 2012 and references within). It is a sedentary fish with a limited home range (Wolfe and Marsden 1998; Ray and Corkum 2001); however, sometimes individuals can move long distances (> 1 km, Wolfe and Marsden 1998). Genetic evidence suggests relatively rapid adjustment to new habitats in the Baltic (Björklund and Almqvist 2010), which may have played a significant role in the species' invasion success. The species' high tolerance of variability in environmental factors, aggressive behavior, varied diet (Charlebois et al. 1997), and reproductive strategy (McInnis and Corkum 2000) likely all contribute to the invasion success.

With such a successful invasion story so far, the relationship between the invasive round goby and native Baltic species needs to be clarified. The role of invasive species within food webs can be defined by whether there are native predators and/or competitors. With many invasive species showing varied diets and high prey consumption rates, direct consumption can have important consequences on native prey populations. Round gobies feed mainly upon molluscs (reviewed by Kornis et al. 2012), and have been shown to exhibit size-selective feeding upon bivalves (e.g. Ghedotti et al 1995; Karlson et al. 2007; Andraso et al. 2011). Fish remains have been detected in large individuals collected in the Baltic Sea (Skora and Rzeznik 2001; Wandzel 2003; Ustups et al. 2015), although fish were a small portion of the diet. In this laboratory-based study, we examined round goby feeding behaviors during

Table 1. Summary of ranges and means (± 1 SE) of round goby metrics for individuals used in feeding behavior trials.

Round Goby Metric	Range	Mean \pm SE
<i>Experiments 1, 2, 3, 5 (N = 11)</i>		
Total Length (mm)	126-157	143.9 \pm 2.8
Weight (g)	30-47.9	40.7 \pm 2.0
Gape Height (mm)	14-18	15.8 \pm 0.4
Gape Width (mm)	13-16	14.5 \pm 0.4
<i>Experiment 4 (N = 5)</i>		
Total Length (mm)	105-165	130.0 \pm 11.2
Weight (g)	13.5-62.4	32.8 \pm 9.0
Gape Height (mm)	7-12	9.2 \pm 0.8
Gape Width (mm)	9-14	11.7 \pm 0.9

consumption of the two most abundant bivalve species of the Northern Baltic Sea (Segerstråle 1944), blue mussels, *Mytilus trossulus* Gould, 1850 and Baltic clams, *Macoma balthica* Linnaeus, 1758, and the native European flounder *Platichthys flesus* Linnaeus, 1758 that has previously been suggested to be a competitor for food (e.g. Skora and Rzeznik 2001; Wandzel 2003; Corkum et al. 2004; Karlson et al. 2007), but not a prey item. The objectives of our experiments were twofold: (1) assess mollusk prey size and species preference of round goby, and (2) determine if round goby will consume juvenile flounder.

Material and methods

Predator and prey species

Round gobies were collected August 20 through mid-September 2014 from two sites in Mariehamn, Finland (60°05'03.0"N 19°55'56.3"E and 60°05'56.4"N 19°55'26.8"E) using crawfish cage traps and small fyke nets (Table 1). This invasive species still has a limited range in the Åland Islands – the first record in Mariehamn, Finland was in 2011 (Michalek et al. 2012) – and these two sites proved successful for round goby capture (>20 captured; only males of a specific size range were used and only 2 females were captured, see Table 1). Upon collection, round gobies were transported to the Husö Biological Station (hereafter referred to as Husö), measured, and allowed to acclimate in holding tanks (1 m \times 1 m) aerated with airstones for at least 5 days before use in trials. Experimental trials only used male round gobies because a sufficient number were collected for experimental use, and they were distinguished from females by the shape of the urogenital papilla (Kornis

Table 2. Summary of experimental designs to assess male round goby prey preference. Experiments 1 – 3 had constant prey biomass whereas experiment 4 had constant prey density.

Exp. #	Predator	# Prey	# Replicates	# Controls (no goby)
1	1 male round goby	16 small <i>M. balthica</i> + 4 large <i>M. balthica</i>	8	2
2	1 male round goby	128 small <i>M. trossulus</i> + 48 large <i>M. trossulus</i>	8	2
3	1 male round goby	8 small <i>M. balthica</i> + 2 large <i>M. balthica</i> + 64 small <i>M. trossulus</i> + 24 small <i>M. trossulus</i>	8	2
4	1 male round goby	39 small <i>M. balthica</i> + 10 large <i>M. balthica</i> + 39 small <i>M. trossulus</i> + 10 large <i>M. trossulus</i>	5	2
5	1 male round goby	1 small flounder + 1 large flounder	10	2

et al. 2012). During the acclimation period, round gobies were fed daily a mixed diet of the known prey items, Baltic clams and blue mussels (e.g., Skora and Rzeznik 2001; Wandzel 2003; Karlson et al. 2007; Järv et al. 2011). Fish were fed to satiation in the evening and uneaten prey items were subsequently removed. Holding tanks were static to protect against further colonization of the species, so water changes were required approximately every 2 days.

Baltic clams were collected from the sediments in Skeppsvik Bay, western Åland, Finland (60°10'22.8"N 19°31'22.8"E) August 19 – 20, 2014. The top layer of substrate (water depth < 1 m) was shoveled and sieved on a 0.5 mm sieve to retain clams, which were then transported to Husö. The second prey species, the blue mussel, was collected by divers at Måsklobb (60°21'12.9"N 19°42'02.3"E) in August and from Gomholm, Hammarland (60°20'42.1"N 19°43'54.9"E), Åland Islands in September. Mussels were collected by towing a small triangular dredge with a small-meshed canvas cod end along the bottom. Clam and mussel prey items were measured and assigned to one of two experimental size classes, and placed in holding tanks (29 × 18.5 cm) equipped with airstones. Water changes were done approximately every 2 days.

Juvenile European flounders were collected with a beach seine with bag at Hinderbengt's viken, Åland (60°09'52.9"N 19°31'52.5"E), on August 22 – 23, 2014. The captured flounders were measured for total length (TL) and width (dorsal to ventral edge of fish with fins compressed) to the nearest mm and assigned to one of two size classes based on the size distribution of the catch: small (24 – 38 mm TL; 10 – 14 mm wide) and large (43 – 50 mm TL; 15 – 20 mm width). Prior to use in trials, juvenile flounder were held in an aerated glass aquarium with a layer of sieved sand. The water was changed every 2 days.

Experimental design

Experiments were conducted at Husö during August and September 2014. Four experiments were conducted with bivalve prey and one with juvenile flounder as prey. The first four experiments were designed to assess bivalve size and species preferences of the round goby. The fifth experiment was conducted to assess the potential for the invasive round goby to consume small European flounders.

All bivalve preference experiments exposed one round goby to different size and species combinations of the bivalve prey (Table 2): two single-species experiments (Exp. 1 and 2) and two mixed-species experiments (Exp. 3, constant prey biomass and Exp. 4, constant prey density), each offering both size classes of bivalve prey. The single-species experiments assessed the preference of round gobies for two size classes of bivalve prey. The mixed-species experiments assessed whether the preferences from the single-species treatments were altered when multiple species and prey sizes were available.

The size of bivalves was measured at the widest point of the shell to categorize the bivalves into two experimental size classes. The widest point was used because previous work with round gobies from the Great Lakes preying on other bivalves (dreissenid mussels) suggested that maximum size consumed was limited by fish gape (e.g. Andraso et al. 2011; Kipp et al. 2012). Clam and mussel morphologies differ, so the widest point of the Baltic clam was the shell length (measured as the widest part across the shell at 90° to the height) and for the blue mussel it was shell height (distance from umbo to ventral valve shell margin). All bivalves were measured and assigned to either a small (6 – 9 mm) or large (10 – 13 mm) size class.

Table 3. Details of the experimental design for experiments 1 – 3 and 4 of the bivalve trials. Constant biomass trials contained ca. 105 mg of dry-weight tissue. Constant density trials contained a total of 98 individual prey items. (S) and (L) refer to small and large size classes, respectively.

Species	Size Class	Dry-Tissue Weight (mg)	Clam:Mussel	# indiv.		Est. Biomass (mg dry wt)		Total Trial Biomass
				(single-sp.)	(mixed-spp.)	(single-sp.)	(mixed-spp.)	
Experiments 1 - 3								
<i>M. balthica</i>	S (6 - 9 mm)	3.34	1:8	16	8	53	27	<i>M. balthica</i> only = 53 + 52 = 105 mg
	L (10 - 13 mm)	12.90	1:12	4	2	52	26	
<i>M. trossulus</i>	S (6 - 9 mm)	0.41		128	64	52	26	<i>M. trossulus</i> only = 52 + 52 = 104 mg
	L (10 - 13 mm)	1.09		48	24	52	26	
Mixed-species = 27 + 26 + 26 + 26 = 105 mg								
Experiment 4								
<i>M. balthica</i>	S (6 - 9 mm)	3.34		n/a	39	n/a	130	
	L (10 - 13 mm)	12.90		n/a	10	n/a	129	
<i>M. trossulus</i>	S (6 - 9 mm)	0.41		n/a	39	n/a	16	
	L (10 - 13 mm)	1.09		n/a	10	n/a	11	

For Exp. 1 – 3, the total biomass offered (ca. 105 mg) was standardized, so the number of prey items (in terms of both size and species) varied (see Table 3). Biomass estimates were obtained from previously published shell height-weight relationships for Baltic clams (Arvai 1997) and blue mussels (Wolowicz et al. 2006) using dry tissue weight from Baltic specimens. Because clams were assigned to a size class based on shell length as opposed to shell height, clams (N = 250) were first subsampled and measured for height and length to produce a regression (shell height = $0.7816 \times (\text{shell length}) + 0.1907$; $R^2 = 0.974$; $n = 250$), which was then used to obtain an estimated biomass for each size class of clams. Blue mussels were measured for shell height as in Wolowicz et al. (2006); thus, no regression was necessary and the published relationship was used directly. After obtaining estimated biomasses for both size classes of each species, the biomass ratio between the two sizes of each species was calculated. For example, we determined how many small-sized mussels were needed to equal the biomass of one small-sized clam. Based on this ratio, the number of individuals needed per treatment to standardize biomass (ca. 105 mg) was determined (Table 3).

Following analysis of the first three bivalve experiments, Exp. 4 was conducted as a follow-up in September. This also was a mixed-species experiment (4 prey options: two species, two size classes) but rather than controlling for biomass, the number of prey items was controlled (Table 3). This experiment was used to rule out the preference of one prey over another solely based on the encounter rate of prey items.

The fifth experiment (N = 10) using flounder prey was designed to assess the potential for small round gobies (Table 1) to consume juvenile European flounder. There was a single treatment with 10 replicates, each offering one round goby two flounder – one of each size class (small vs. large).

Bivalve experimental trials: Experiments 1 – 4

Bivalve Exp. 1 – 3 were conducted in 40 L (40 × 30 cm) opaque plastic aquaria with rounded corners. A 2.5 cm layer of 0.5 mm sieved sand was placed on the bottom as substrate, seawater was added to 20 cm depth, and the sand was smoothed to form a level surface. A small clay flower pot (diameter = 11 cm) was placed on its side in one corner of each tank to provide cover for the fish. Round gobies were fasted 24 h prior to the start of trials and all trials were conducted from 20:00 – 08:00 because round gobies can feed nocturnally (Leach 1995; Naddafi and Rudstam 2013). About 2.5 h prior to trials, bivalve prey items were haphazardly added to the experimental tanks to acclimate. Previous studies suggest 1–3 h is sufficient for bivalve acclimation (Dubs and Corkum 1996; Karlson et al. 2007). A single round goby was then introduced and allowed to forage overnight. The round goby was then removed, water was siphoned, and the sand was sieved on a 0.5 mm sieve to collect remaining prey items. The number of whole and crushed prey items of each species and size class was counted and photo-documented. Bivalve prey items that were alive and intact were classified as “surviving” whereas prey items that were crushed but still contained the flesh of the animal were termed

“crushed”. Upon completion of trials and after enumeration of remaining prey, experimental tanks were set up for the next round of trials. Because we conducted 24 trials (8 clam only, 8 mussel only, 8 mixed-species) and only had 11 round gobies within our desired size range, each fish was used twice and two fish were used a third time, while randomizing fish for all trials. All round gobies were returned to the holding tank for 2 nights before use in subsequent trials.

In addition to the experimental trials, recovery controls were conducted for each experiment to confirm that bivalve prey recovery depended on round goby consumption. Two recovery controls were conducted for each of Exp. 1 – 3. Prey items were added to the experimental tank, allowed to acclimate 7 h, and recovered. Recovery was 100% for all control trials. Average (\pm SE) water quality conditions for Exp. 1–3 and 5 were: temperature = $15.5 \pm 0.7^\circ\text{C}$; salinity = 4.85 ± 0.2 ; pH = 7.55 ± 0.04 ; turbidity = 0.65 ± 0.1 NTU; and dissolved oxygen saturation = $65.18 \pm 4.6\%$.

Bivalve Exp. 4 (constant number of prey items) was conducted in mid-September. These trials were designed to assess round goby feeding behavior in relation to prey size and species, when the number of individuals, and thus density, is constant across species, but varies between size classes. The equipment and experimental design were the same as Exp. 1 – 3 with the exception that trials were conducted between 21:00 and 09:00, and the fish meristics were slightly different (Table 1). Five different gobies were used for the five replicates. Water quality conditions were: temperature = 13.6°C ; salinity = 5.14; pH = 7.94; turbidity = 1.23 NTU; and dissolved oxygen saturation = 102.97%.

Flounder experimental trials: Experiment 5

Flounder predation trials were conducted in a similar manner to bivalve trials. Flounder prey were not acclimated to the aquaria beforehand; instead, a single round goby was placed into each tank about 36 h prior to the start of trials. Ten of the 11 gobies used in Exp. 1 – 3 were used once each for the flounder experimental trials. Round gobies were fed blue mussels the first night in the aquaria and then fasted for 24 h. Prior to commencing trials, the tanks were inspected to ensure no mussels were left behind from the first night’s feeding. The addition of one flounder of each size class marked the initiation of a trial and round gobies were allowed to forage from 20:00 – 08:00. When introduced to the experimental tanks, flounders typically moved to the opposite side of the tank from the round goby. At the

completion of each trial, the round goby was removed and a small net was used to collect any remaining flounder. If the flounder were not collected by the net, the water was siphoned, and the sand was sieved on a 0.5 mm sieve. To confirm flounder consumption from trials where at least one flounder was not recovered, two round gobies were killed and the entire digestive tract was removed and analyzed. Additionally, two recovery controls (no goby present) were conducted – one flounder of each size class was added to the experimental tank, acclimated 7 h and subsequently recovered – recovery was 100%.

Statistical analyses

Round goby bivalve prey selectivity was analyzed separately for single-species and mixed-species trials using Manly’s selectivity index α (Manly 1974; Chesson 1983), an index that does not change with differences in food densities, unless consumer behaviors also differ:

$$\alpha_i = \frac{\ln((n_{i0} - r_i)/n_{i0})}{\sum_{j=1}^m \ln(\frac{n_{j0} - r_j}{n_{j0}})}$$

where n_{i0} is the number of prey items initially stocked of type i , r_i is the number of prey items of type i consumed by the predator, and m is the number of prey types available in the experiment.

For single-species trials, $m = 2$, because two prey types were used (small and large size class). For mixed-species trials, $m = 4$, because four prey types were available (two species of bivalve, two size classes). If the predator consumed all individuals of the most preferred prey, the equation was modified as in Klecka and Boukal (2012), by adding a single individual of that particular prey to the corresponding n_{i0} and n_{j0} . This provides a slightly conservative estimate of α_i by assuming the added individual would have survived. Values of α_i ranged from 0 to 1 with 0 being complete avoidance, 1 being complete preference. When $\alpha_i > 1/m$, there is selection for the particular prey type. Likewise, when $\alpha_i < 1/m$, there is selection against. If $\alpha_i = 1/m$, there is no selection and the predator is feeding randomly. As suggested by Manly (1995), we then compared values of the selectivity index with values expected for no selectivity using separate t-tests with Bonferroni-corrected p-values to account for multiple t-tests.

Only blue mussels were left crushed frequently enough for statistical analysis (281 blue mussels crushed; 3 clams crushed). The number of small and large crushed blue mussels remaining in single-species and mixed-species trials were compared by

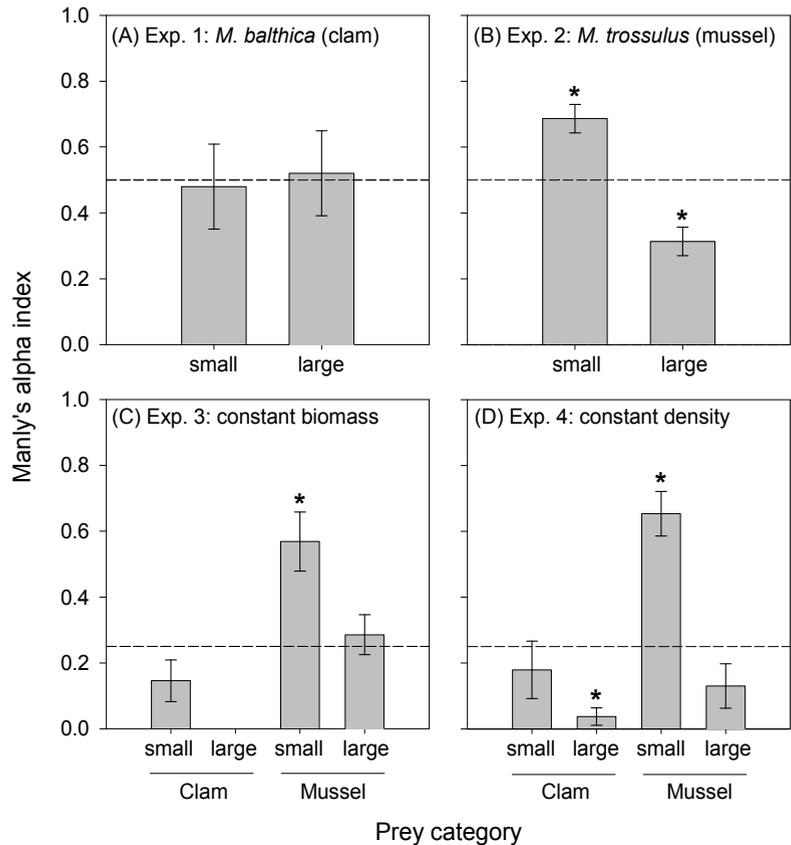


Figure 1. Selection index of small and large clams (A), mussels (B), and both species (C, D) for male round gobies. Values above the dashed horizontal line indicate selection for size and species of bivalve. Asterisks indicate statistically significant selection (for or against) after Bonferroni corrections. Data are presented as mean \pm SE.

separate t-tests (Exp. 1–3) or non-parametric Wilcoxon tests (Exp. 4) after a $\log(x+1)$ data transformation. For the flounder experimental trials, a simple logistic regression was used to analyze the predictive power of flounder body width for flounder consumption by round goby. The dependent variable was flounder consumption (or recovery) and the independent variable was flounder width (a potential limiting factor for goby gape size). Flounder predation analyses were performed in SigmaPlot 11; results were considered significant at $\alpha = 0.05$.

Results

Male round gobies did not have a size preference for *M. balthica* but did seem to prefer small mussels (Figure 1). Gobies selected for small mussels when only small and large mussels were offered, and this result persisted in the mixed-species trials regardless of whether prey were presented as constant biomass or constant density. Round gobies also selected

against large mussels in the mussel-only experiment (Exp. 2) and against large clams in Exp. 4. The number of crushed bivalves remaining supported the results of prey preference: more small mussels were crushed in single-species trials ($t = 3.161$; $p = 0.0072$) (Figure 2A) and a similar number of small and large mussels were crushed in mixed-species trials ($p > 0.05$) (Figure 2B, C).

In flounder consumption trials, male round gobies consumed all but one small-bodied juvenile flounder and 100% of the larger flounder were recovered from the experimental tanks. Although no large flounder were consumed, they were visibly damaged (bitten tails, torn fins, internal bleeding) and either in poor condition (exhaustion, little movement) or dead. Flounder recovery was positively correlated with flounder width ($\beta = 0.866$; Wald = 5.358; $p = 0.021$; Figure 3) – flounders >14 mm wide were not consumed (Figure 3). The digestive tract examination of two round gobies confirmed the presence of flounder remains within the digestive tract.

Discussion

Small male round gobies demonstrated size- and species-selectivity when fed bivalves. Round gobies preferred mussels over clams whether biomass or density was held constant, suggesting encounter rates were not the driving factor for the species preference. Previous laboratory experiments (Karlson et al. 2007) and stomach content analyses of round gobies (e.g. Skora and Rzeznik 2001; Wandzel 2003; Järv et al. 2011) have both indicated blue mussels to be an important diet component in the Baltic Sea. Furthermore, size-selectivity of bivalve prey items is not uncommon for round gobies (Ghedotti et al. 1995; Karlson et al. 2007; Andraso et al. 2011). Size-selectivity of bivalve prey may be influenced by traits of both predator and prey. In terms of the predator, prey selectivity can be physically determined with mouth or throat morphology placing an upper limit on prey size that can be ingested (e.g. Lawrence 1957; Hartman 1958). Bivalve prey characteristics that may influence size-selectivity include behavior, size, morphology and thickness of the shell.

Optimal foraging theory predicts, among other things, that a predator will consume prey that provides the most energetic value for the time it takes to locate, obtain, and feed on that prey item (Hughes 1980). Overall, small (6–9 mm) blue mussels were preferred by small round gobies, even though their biomass was the least of the prey items offered. Although their biomass was very small, small mussels may have been the easiest prey to find and consume (i.e. there was less handling time) since the mussels were not strongly attached to any surface with their byssal threads and none of the mussels buried into the sand. Baltic clams, on the other hand, buried into the sand and were presumably not as readily available to the round gobies without allocating time and effort to searching. Additionally, multiple small blue mussels may be consumed at any given time (e.g., Naddafi and Rudstam 2013) so when a round goby encounters a patch of small blue mussels (typical for mussels with byssal threads), many can be taken in at once as opposed to having to find individual Baltic clams (less clustered than blue mussels).

Consumption of blue mussels was as high as 82 small or 20 large mussels per 12 h but daily consumption may be higher. The round gobies (105 – 165 mm TL) in our trials consumed ~3.3 mg/h (ash free dry weight) while animals 65 – 80 mm standard length from the Laurentian Great Lakes consumed dreissenid mussels at a rate of ~12 mg/h dry weight during laboratory experiments (Diggins et al. 2002). Alternatively, consumption could be lower in natural

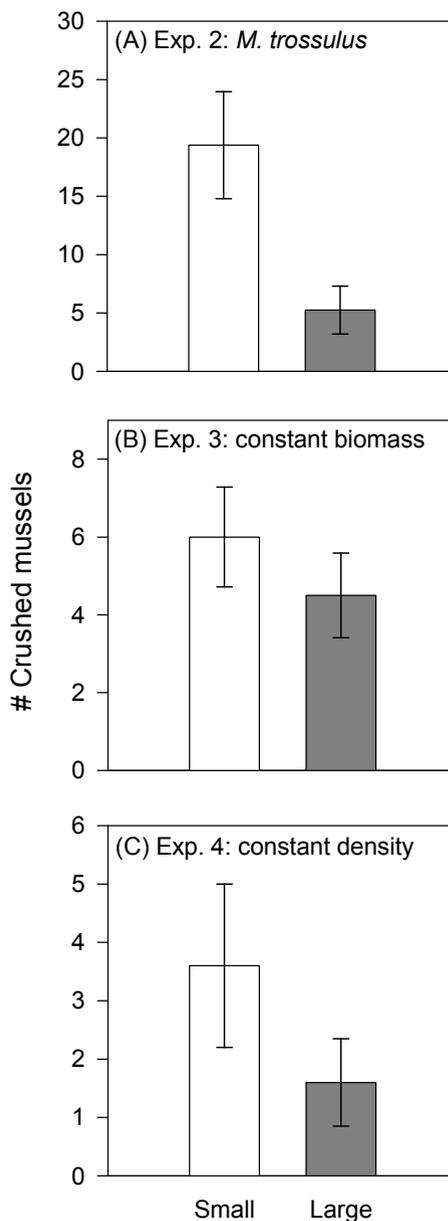


Figure 2. Mean (± 1 SE) number of crushed mussels remaining in single-species (A) and mixed-species (B, C) experiments. Note the scale differences.

settings since male round gobies would be performing other activities like nest guarding and territory defense.

Round gobies seem to prefer blue mussels over clams; consequently, blue mussel populations are probably more at risk for consumption than Baltic clams in our study area. Additionally, round gobies are territorial and do not typically move far from their home range (Ray and Corkum 2001; Björklund and Almqvist 2010; Cerwenka et al. 2014) so consumption effects may be exacerbated in areas

where round gobies are locally abundant. Due to the rather recent (2011) colonization of the Åland Islands by round gobies, we would not expect round gobies to have a noticeable impact on their blue mussel populations until goby abundance increases to some threshold level.

Round gobies are potential competitors for food resources (Baltic clams) with native Baltic flounder species (e.g. Karlson et al. 2007). Round gobies also have the potential to directly impact native flounder by consuming them. Fish remains typically are reported as being a small portion of the round goby diet (French and Jude 2001; Carman et al. 2006; Karlson et al. 2007; Ustups et al. 2015). Our results demonstrated that small male round gobies readily ate small juvenile flounders. From the two animals examined in 12 h trials, the remains were well-digested (only bones and soft tissue remained) and found near the end of the digestive tract. Almost complete digestion within 12 h may be one explanation for why diet studies of the round goby report low amounts of fish consumed, which suggests the effects of round goby predation on small native fish species may be underestimated.

The small male round gobies in our study did not consume flounders >14 mm body width although larger individuals were damaged or killed. The consumption of smaller flounder individuals is consistent with gape-limited predation. The maximum gape width and gape height of our gobies was 16 and 18 mm, respectively. The larger flounders offered as prey averaged 18.2 mm body width and thus were larger than the maximum gape widths of the gobies in our experiments. Nevertheless, the round gobies still damaged or killed the largest flounders offered, possibly an attempt to eat them or as a result of territorial behavior by these male gobies. Similar experiments with female round gobies may not yield the same results.

Multiple laboratory experiments showed that the invasive round goby can have direct consumptive effects on the nearshore fauna in the Baltic Sea. Small male round gobies readily consumed small blue mussels and lesser amounts of Baltic clams, both of which are common prey items for native fish species. While the small gobies used in our experiments preyed preferentially on small blue mussels, larger-sized gobies will eat larger sized mussels in addition to the small-sized mussels (e.g. Karlson et al. 2007), suggesting there may not be a size refuge for blue mussels. Additional research into the invasive success and population sizes of round gobies in this area, as well as their natural feeding rates for blue mussels could help understand any potential threat to the local blue mussel population.

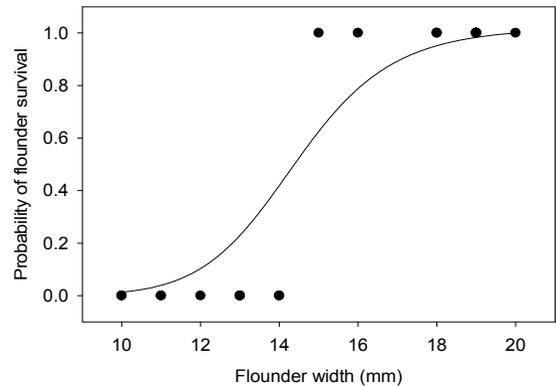


Figure 3. Logistic regressions for the probability of flounder survival vs. flounder width when flounder were presented to male round gobies.

Round gobies also directly consumed small European flounder, a commercially important species in the area. As round gobies further establish themselves in the area and potentially begin to overlap habitats with flounder, this invasive species may not only have an indirect effect on native flounder populations through food competition but may also have a direct effect through consumption of the flounder themselves, both of which have the potential to negatively affect the commercial fishery.

Acknowledgements

We extend our thanks to J. Nyström, M. Kennedy, and A. Macy for prey collection assistance, and T. Cederberg for water quality data. We are grateful to the Department of Marine Sciences at the University of South Alabama for supporting the travel of MNS, LCS, and BK. We thank our colleagues at Husö Biological Station for advice and assistance with our experiments and three anonymous reviewers whose suggestions greatly improved this manuscript.

References

- Andraso GM, Ganger MT, Adamczyk J (2011) Size-selective predation by round gobies (*Neogobius melanostomus*) on dreissenid mussels in the field. *Journal of Great Lakes Research* 37: 298–304, <http://dx.doi.org/10.1016/j.jglr.2011.02.006>
- Arvai JL (1997) The population dynamics and production of *Corophium salmonis* (S.) and *Macoma balthica* (L.) on an estuarine mudflat in response to effluent diversion from a sewage plant, Sturgeon Bank, British Columbia. MSc Thesis, University of British Columbia, Vancouver, British Columbia, Canada, 249 pp
- Björklund M, Almquist G (2010) Rapid spatial genetic differentiation in an invasive species, the round goby *Neogobius melanostomus* in the Baltic Sea. *Biological Invasions* 12: 2609–2618, <http://dx.doi.org/10.1007/s10530-009-9669-z>
- Carlton JT (1996) Pattern, process and prediction in marine invasive ecology. *Biological Conservation* 78: 97–106, [http://dx.doi.org/10.1016/0006-3207\(96\)00020-1](http://dx.doi.org/10.1016/0006-3207(96)00020-1)
- Carman SM, Janssen J, Jude DJ, Berg MB (2006) Diel interactions between prey behavior and feeding in an invasive fish, the round goby, in a North American river. *Freshwater Biology* 51: 742–755, <http://dx.doi.org/10.1111/j.1365-2427.2006.01527.x>

- Casini M (2013) Spatio-temporal ecosystem shifts in the Baltic Sea: top-down control and reversibility potential. In: Daniels JA (ed), *Advances in Environmental Research* 28, pp 149–167
- Cerwenka AF, Brandner J, Geist J, Schliewen UK (2014) Strong versus weak population genetic differentiation after a recent invasion of gobiid fishes (*Neogobius melanostomus* and *Ponticola kessleri*) in the upper Danube. *Aquatic Invasions* 9: 71–86, <http://dx.doi.org/10.3391/ai.2014.9.1.06>
- Charlebois PM, Marsden JE, Goettel RG, Wolfe RK, Jude DJ, Rudnicka S (1997) The Round goby, *Neogobius melanostomus* (Pallas), a review of European and North-American literature. Illinois-Indiana Sea Grant Program and Illinois Natural History Survey INHS Special Publication No 20, 76 pp
- Chesson J (1983) The estimation and analyses of preference and its relation to foraging models. *Ecology* 64: 1297–1304, <http://dx.doi.org/10.2307/1937838>
- Corkum LD, Sapota MR, Skora KE (2004) The round goby, *Neogobius melanostomus*, a fish invader on both sides of the Atlantic Ocean. *Biological Invasions* 6: 173–181, <http://dx.doi.org/10.1023/B:BINV.0000022136.43502.db>
- Diggins TP, Kaur J, Chakraborti RK, DePinto JV (2002) Diet choice by the exotic round goby (*Neogobius melanostomus*) as influenced by prey motility and environmental complexity. *Journal of Great Lakes Research* 28: 411–420, [http://dx.doi.org/10.1016/S0380-1330\(02\)70594-7](http://dx.doi.org/10.1016/S0380-1330(02)70594-7)
- Dubs DO, Corkum LD (1996) Behavioral interactions between round gobies (*Neogobius melanostomus* and mottled sculpins (*Cottus bairdi*). *Journal of Great Lakes Research* 22: 838–844, [http://dx.doi.org/10.1016/S0380-1330\(96\)71005-5](http://dx.doi.org/10.1016/S0380-1330(96)71005-5)
- Eriksson BK, Ljunggren L, Sandström A, Johansson G, Mattila J, Rubach A, Råberg S, Snickars M (2009) Declines in predatory fish promote bloom-forming macroalgae. *Ecological Applications* 19: 1975–1988, <http://dx.doi.org/10.1890/08-0964.1>
- French III JR, Jude DJ (2001) Diets and diet overlap of nonindigenous gobies and small benthic native fishes co-inhabiting the St. Clair River, Michigan. *Journal of Great Lakes Research* 27: 300–311, [http://dx.doi.org/10.1016/S0380-1330\(01\)70645-4](http://dx.doi.org/10.1016/S0380-1330(01)70645-4)
- Ghedotti MJ, Smihula JC, Smith GR (1995) Zebra mussel predation by round gobies in the laboratory. *Journal of Great Lakes Research* 21: 665–669, [http://dx.doi.org/10.1016/S0380-1330\(95\)71076-0](http://dx.doi.org/10.1016/S0380-1330(95)71076-0)
- Hartman GF (1958) Mouth size and food size in young Rainbow Trout, *Salmo gairdneri*. *Copeia* 1958: 233–234, <http://dx.doi.org/10.2307/1440608>
- Hughes RN (1980) Optimal foraging theory in the marine context. *Annual Review of Marine Biology and Oceanography* 18: 423–481
- Järv L, Kotta J, Kotta I, Raid T (2011) Linking the structure of benthic invertebrate communities and the diet of native and invasive fish species in a brackish water ecosystem. *Annales Zoologici Fennici* 48: 129–141, <http://dx.doi.org/10.5735/086.048.0301>
- Karlson AML, Almqvist G, Skora KE, Appelberg M (2007) Indications of competition between non-indigenous round goby and native flounder in the Baltic Sea. *ICES Journal of Marine Science* 64: 479–486, <http://dx.doi.org/10.1093/icesjms/fsi049>
- Kautsky L, Svensson S (2003) Life in the Baltic Sea. In: Rydén L, Migula P, Anderson M (eds), *Environmental Science: understanding, protecting and managing the environment in the Baltic Sea Region*. Baltic University Press, Uppsala, pp 149–181
- Kipp R, Hébert I, Lacharité M, Ricciardi A (2012) Impacts of predation by the Eurasian round goby (*Neogobius melanostomus*) on molluscs in the upper St. Lawrence River. *Journal of Great Lakes Research* 38: 78–89, <http://dx.doi.org/10.1016/j.jglr.2011.11.012>
- Klecka J, Boukal DS (2012) Who eats whom in a pool? A comparative study of prey selectivity by predatory aquatic insects. *PLoS ONE* 7: e37741, <http://dx.doi.org/10.1371/journal.pone.0037741>
- Kornis MS, Mercado-Silva N, Vander Zanden MJ (2012) Twenty years of invasion a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. *Journal of Fish Biology* 80: 235–285, <http://dx.doi.org/10.1111/j.1095-8649.2011.03157.x>
- Lawrence JM (1957) Estimated sizes of various forage fishes largemouth bass can swallow. In: Proceedings of the Fourteenth Annual Conference, Southeastern Association of Game and Fish Commissioners. Biloxi, Mississippi, USA, October 23–26, 1960, pp 220–226
- Leach JH (1995) Non-indigenous species in the Great Lakes: were colonization and damage to ecosystem health predictable? *Journal of Aquatic Ecosystem Health* 4: 117–128, <http://dx.doi.org/10.1007/BF00044795>
- Manly BF (1974) A model for certain types of selection experiments. *Biometrics* 30: 281–294, <http://dx.doi.org/10.2307/2529649>
- Manly BF (1995) Measuring selectivity from multiple choice feeding-preference experiments. *Biometrics* 51: 709–715, <http://dx.doi.org/10.2307/2532956>
- McInnis AJ, Corkum LD (2000) Fecundity and reproductive seasons of the round goby *Neogobius melanostomus* in the Upper Detroit River. *Transactions of the American Fisheries Society* 129: 136–144, [http://dx.doi.org/10.1577/1548-8659\(2000\)129<0136:FARS OT>2.0.CO;2](http://dx.doi.org/10.1577/1548-8659(2000)129<0136:FARS OT>2.0.CO;2)
- Michalek M, Puntila R, Strake S, Werner M (2012) Abundance and distribution of round goby (*Neogobius melanostomus*). HELCOM Baltic Sea Environment Fact Sheets. <http://www.helcom.fi/baltic-sea-trends/environment-fact-sheets/> (accessed 2 September 2014)
- Naddafi R, Rudstam LG (2013) Predation on invasive zebra mussel, *Dreissena polymorpha*, by pumpkinseed sunfish, rusty crayfish, and round goby. *Hydrobiologia* 721: 107–115, <http://dx.doi.org/10.1007/s10750-013-1653-z>
- Ojaveer H (2006) The round goby, *Neogobius melanostomus*, is colonizing the NE Baltic Sea. *Aquatic Invasions* 1: 44–45, <http://dx.doi.org/10.3391/ai.2006.1.1.11>
- Ray WJ, Corkum LD (2001) Habitat and site affinity of the Round goby. *Journal of Great Lakes Research* 27: 329–334, [http://dx.doi.org/10.1016/S0380-1330\(01\)70648-X](http://dx.doi.org/10.1016/S0380-1330(01)70648-X)
- Ruiz G, Carlton J, Grosholz E, Hines A (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent and consequences. *American Zoologist* 37: 621–632, <http://dx.doi.org/10.1093/icb/37.6.621>
- Seegerstråle SG (1944) [translated from German] A contribution to the knowledge of the eastern distribution of blue mussels (*Mytilus edulis* L.) along the southern coast of Finland. *Journal of the Society of Flora and Fauna of Finland and Scandinavia* 19: 5–7
- Skora KE, Rzeznik J (2001) Observation on diet composition of *Neogobius melanostomus* Pallas 1811 (Gobiidae, Pisces) in the Gulf of Gdansk (Baltic Sea). *Journal of Great Lakes Research* 27: 290–299, [http://dx.doi.org/10.1016/S0380-1330\(01\)70644-2](http://dx.doi.org/10.1016/S0380-1330(01)70644-2)
- Ustups D, Bergström U, Florin AB, Kruze E, Zilniece D, Elferts D, Knospina A, Uzars D (2015) Diet overlap between juvenile flatfish and the invasive round goby in the central Baltic Sea. *Journal of Sea Research* 107: 121–129, <http://dx.doi.org/10.1016/j.seares.2015.06.021>
- Voipio A (1981) The Baltic Sea. Elsevier Oceanography Series 30, Elsevier, Amsterdam, pp 123–175
- Wandzel T (2003) The food and feeding of the round goby (*Neogobius melanostomus* Pallas, 1811) from the Puck Bay and the Gulf of Gdańsk. *Bulletin of the Sea Fisheries Institute*, 1: 23–39.
- Wolfe RK, Marsden JE (1998) Tagging methods for the round goby (*Neogobius melanostomus*). *Journal of Great Lakes Research* 24: 731–735, [http://dx.doi.org/10.1016/S0380-1330\(98\)70857-3](http://dx.doi.org/10.1016/S0380-1330(98)70857-3)
- Wolowicz M, Sokolowski A, Salem Bawazir A, Lasota R (2006) Effect of eutrophication on the distribution and ecophysiology of the mussel *Mytilus trossulus* (Bivalvia) in the southern Baltic Sea (the Gulf of Gdańsk). *Limnology and Oceanography* 51: 580–590, http://dx.doi.org/10.4319/lo.2006.51.1_part_2.0580
- Zaiko A, Lehtiniemi M, Narčiūsis A, Olenin S (2011) Assessment of bioinvasion impacts on a regional scale: a comparative approach. *Biological Invasions* 13: 1739–1765, <http://dx.doi.org/10.1007/s10530-010-9928-z>